

# The cranial endocast of *Dipnorhynchus sussmilchi* (Sarcopterygii: Dipnoi) and the interrelationships of stem-group lungfishes

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The first virtual cranial endocast of a lungfish from the Early Devonian, *Dipnorhynchus sussmilchi*, is described. *Dipnorhynchus*, only the fourth Devonian lungfish for which a near complete cranial endocast is known, is a key taxon for clarifying primitive character states within the group. A ventrally-expanded telencephalic cavity is present in the endocast of *Dipnorhynchus* demonstrating that this is the primitive state for the Dipnoi. *Dipnorhynchus* also possesses a utricular recess differentiated from the sacculolagenar pouch like that seen in stratigraphically younger lungfish (*Dipterus*, *Chirodipterus*, *Rhinodipterus*), but absent from the dipnomorph *Youngolepis*. We do not find separate pineal and para-pineal canals in contrast to a reconstruction from previous authors. We conduct the first phylogenetic analysis of Dipnoi based purely on endocast characters, which supports a basal placement of *Dipnorhynchus* within the dipnoan stem group, in agreement with recent analyses. Our analysis demonstrates the value of endocast characters for inferring phylogenetic relationships.

1           **The cranial endocast of *Dipnorhynchus sussmilchi***  
2           **(Sarcopterygii: Dipnoi) and the interrelationships of stem-**  
3           **group lungfishes**

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16           **ABSTRACT**

17           The first virtual cranial endocast of a lungfish from the Early Devonian, *Dipnorhynchus*  
18           *sussmilchi*, is described. *Dipnorhynchus*, only the fourth Devonian lungfish for which a near  
19           complete cranial endocast is known, is a key taxon for clarifying primitive character states within  
20           the group. A ventrally-expanded telencephalic cavity is present in the endocast of  
21           *Dipnorhynchus* demonstrating that this is the primitive state for the Dipnoi. *Dipnorhynchus* also  
22           possesses a utricular recess differentiated from the sacculolagenar pouch like that seen in  
23           stratigraphically younger lungfish (*Dipterus*, *Chirodipterus*, *Rhinodipterus*), but absent from the  
24           dipnomorph *Youngolepis*. We do not find separate pineal and para-pineal canals in contrast to a  
25           reconstruction from previous authors. We conduct the first phylogenetic analysis of Dipnoi based  
26           purely on endocast characters, which supports a basal placement of *Dipnorhynchus* within the  
27           dipnoan stem group, in agreement with recent analyses. Our analysis demonstrates the value of  
28           endocast characters for inferring phylogenetic relationships.

## 31 INTRODUCTION

32 Lungfish, or dipnoans as they are also known, have origins dating back over 400 million years.  
33 Today there are just six extant species, but it was during the Devonian Period that they reached  
34 the peak of their success and diversity (Clack et al. 2011). ‘Total-group’ lungfishes are a well-  
35 supported monophyletic group, but early dipnoan phylogeny has long been contentious and  
36 remains unresolved (Johanson & Ahlberg 2011). Campbell and Barwick (1990) employed a  
37 functional-adaptive method, splitting Palaeozoic lungfishes into three lineages based mainly on  
38 dental characters (tooth-plated, dentine-plated and denticulated forms). However, most workers  
39 in the field instead utilise cladistic methods; applying the principles of either parsimony (Ahlberg  
40 et al. 2006; Clement 2012; Marshall 1986; Miles 1977; Qiao & Zhu 2009; Schultze & Marshall  
41 1993) or Bayesian inference (Friedman 2007).

42

43 The split between the extant lungfish families is thought to have occurred in the Permian  
44 (Heinicke et al. 2009). In general terms this means that ‘crown-group’ lungfishes contains all the  
45 living representatives and their last common ancestor (of plausible Permian age), and all of the  
46 (both fossil and living) descendants of that ancestor. Thus, ‘stem-group’ lungfish is equivalent to  
47 the total group minus the crown group, and contains all of the Devonian lungfishes. The most  
48 unambiguous basal member of the lungfish stem group (and sister group to all other lungfishes)  
49 is *Diabolepis* from the Lower Devonian of China (Chang 1995; Chang & Yu 1984), although  
50 some authors disagree with this interpretation (Campbell & Barwick 2001). The group is thought  
51 to have radiated quickly (Lloyd et al. 2011), and early Devonian lungfishes are known from  
52 deposits across China, Russia, Europe, North America and Australia (Campbell & Barwick  
53 1986). The Australian fauna from this time is dominated by the robust, short-headed  
54 ‘dipnorhynchid’ taxa, typified by *Dipnorhynchus* itself (Etheridge 1906).

55

56 Material of the Early Devonian genus *Dipnorhynchus* was first described over a century ago, and  
57 although the name ‘*Ganorhynchus*’ was originally used (Etheridge 1906), ‘*Dipnorhynchus*’ was  
58 erected two decades later for *D. susmilchi* (Jaekel 1927). *Dipnorhynchus susmilchi* (Campbell  
59 & Barwick 1982a) is known from the Taemas – Wee Jasper limestones that occur around  
60 Burrinjuck Dam in New South Wales, Australia (see Figure 1), and have been dated as Emsian in  
61 age (Thomson & Campbell 1971). Other dipnoan taxa described from the same site include

62 *Dipnorhynchus kurikae* (Campbell & Barwick 2000), *Speonesydrion iani* (Campbell & Barwick  
63 1983), and *Cathlorhynchus trismodipterus* (Campbell et al. 2009). Furthermore, there is an  
64 additional *Dipnorhynchus* species known from a locality about 200 km south of the Taemas –  
65 Wee Jasper limestones, *D. kiandrensis* (Campbell & Barwick 1982b).

66

67 The skull roof and associated cranial material of *D. sussmilchi* was first described in some detail  
68 (Hills 1941), and then later elaborated upon (Campbell 1965; Thomson & Campbell 1971).  
69 However a thorough investigation of braincase material for the genus did not come until later  
70 when Campbell and Barwick (1982a) described the neurocranium and reconstructed the  
71 endocranial cavity of *D. sussmilchi*. This was achieved by examining broken specimens to reveal  
72 internal anatomy, or by using soft fishing wire to trace the course of small canals. Later, similar  
73 treatment for *D. kurikae* ensued (Campbell & Barwick 2000). Further details regarding the  
74 neurocranium and space for the endolymphatic ducts and labyrinth of *D. sussmilchi* shortly  
75 followed (Campbell et al. 2000).

76

77 With the increasing accessibility of modern, non-invasive scanning technology such as  
78 synchrotron and micro-computed tomography ( $\mu$ CT), along with more sophisticated software  
79 packages for data processing and visualization, the field of palaeoneurology seems to be  
80 undergoing an upsurge (Walsh et al. 2013). Until relatively recently, researchers had to rely upon  
81 fortuitous findings of damaged skulls, or resort to destructive techniques (Stensiö 1963) to  
82 examine the internal anatomy of the braincase. These more traditional techniques have been  
83 shown to be somewhat limited, especially with respect to fine morphological details (Giles et al.  
84 2016). However, today we are quickly increasing the number of taxa for which virtual cranial  
85 endocast morphology is known across all vertebrate groups (Balanoff et al. 2015; Falk 2012; Lu  
86 et al. 2012), including fishes such as the sarcopterygian *Powichthys* (Clément & Ahlberg 2010),  
87 the placoderm *Romundina* (Dupret et al. 2014), the galeaspid *Shuyu* (Gai et al. 2011),  
88 actinopterygians (Giles & Friedman 2014; Giles et al. 2016; Lu et al. 2016a), and  
89 chondrichthyans (Maisey 2007).

90

91 *Chirodipterus wildungensis* from the Upper Devonian of Germany was the first cranial endocast  
92 of a lungfish published (Säve-Söderbergh 1952), although this was drawn from a single damaged

93 specimen and provided only a relatively crude reconstruction. Other examples include a partial  
94 endocast of the Late Devonian *Holodipterus* (Pridmore et al. 1994), as well as those of  
95 *Dipnorhynchus* (Campbell & Barwick 1982a; Campbell & Barwick 2000). Although the first  
96 virtual lungfish endocasts only came recently, they have greatly enriched our knowledge of the  
97 field. Not only are the tomographic methods that produce these endocasts non-destructive, they  
98 also provide far more comprehensive information about the cranial cavity, and far superior  
99 possibilities for visualization than traditional techniques. Two genera have been investigated by  
100 tomography to date: the Late Devonian *Rhinodipterus* from Australia (Clement & Ahlberg 2014)  
101 and *Dipterus* from the Middle Devonian of Scotland (Challands 2015). Further to this, the brain  
102 and endocast of the extant Australian lungfish, *Neoceratodus*, is also known from CT data  
103 (Clement et al. 2015), and researchers are developing techniques for reconstructing brains in  
104 extinct members (Clement et al. 2016). Not only are cranial endocasts rich sources of  
105 morphological data in their own right, they can also give clues as to an animal's brain structure,  
106 sensory abilities and inferred behavior.

107

108 We expand on this growing body of work by investigating the cranial endocast of  
109 *Dipnorhynchus susmilchi* from the Early Devonian of Australia as revealed from tomographic  
110 data. Our work represents the oldest, and only the fourth lungfish taxon endocast investigated,  
111 and is the currently the only example from the Early Devonian. The data from *Dipnorhynchus*  
112 contributes to uncovering how the lungfish brain has evolved through time, and also provides  
113 valuable data in resolving early dipnoan phylogeny.

114

115

## 116 MATERIAL & METHODS

117 The *Dipnorhynchus susmilchi* Etheridge (1906) specimen (ANU 18815) is a well-preserved,  
118 acid-prepared complete cranium from the Early Devonian (Emsian) Taemas-Wee  
119 Jasper/Burrinjuck limestones of New South Wales, Australia (Fig. 1). The specimen is housed at  
120 the Australian National University, Canberra, Australia, and was scanned at the High Resolution  
121 X-ray Computed Tomography ( $\mu$ CT) facility of the same location (Sakellariou et al. 2004) with a  
122 voxel resolution of 30.4 microns. The ANU  $\mu$ CT facility is based on cone beam geometry and  
123 has a detector pixel width of 2048 pixels. The original scan was performed with a focus on snout

124 morphology for another study (Campbell et al. 2010), and consequently the rear portion of the  
125 skull was not captured.

126

127 *VGStudio Max*, version 2.2 (Volume Graphics Inc., Germany) was used to achieve three-  
128 dimensional segmentation and modeling of the cranial endocast through a combination of  
129 manual segmentation and thresholding. The resulting endocast model was smoothed by a factor  
130 of three prior to export.

131

132 We assembled our character matrix of 20 characters and 10 taxa in *Mesquite 3.01* (see  
133 Supplementary Information for full details). Characters 1-13 were taken from previous analyses  
134 (Friedman 2007; Giles et al. 2015), however 14-20 are new characters identified through the  
135 course of this study. The parsimony analysis was conducted using the heuristic search algorithm  
136 in *PAUP v4.0b10* (Swofford 2001) using stepwise addition, 10,000 random addition sequence  
137 replicates holding five trees at each step, with tree bisection and reconnection (TBR) enabled,  
138 and automatically increasing maxtrees by 100. The Late Devonian coelacanth *Diplocercides* was  
139 designated as the outgroup. Bootstrap values were then calculated using 1000 random replicates  
140 of the heuristic search in PAUP, again with TBR enabled for 10 replicates.

141

142

## 143 **RESULTS**

### 144 **Description**

145 The skull measures 24 cm across the quadrates at its widest point, and with a height of 20 cm  
146 from the base of the quadrate to the top of the skull roof. The scan data extends from the tip of  
147 the snout to the mid-point of the labyrinth region. The endocast itself (Figs 2-5) measures 13.5  
148 cm across the widest points of the horizontal semicircular canals, and 26 cm from the anterior-  
149 most point of the nasal capsules to the junction between the posterior and anterior semicircular  
150 canals. Unfortunately the occipital region of the specimen is not included in the scan.

151 Proportionally the nasal capsules are the longest structures of the available endocast being  
152 approximately 25% of the total length. The metencephalic and telencephalic regions account for  
153 10-15% endocast length, the diencephalic <10% and the mesencephalic cavity, at ~5% total  
154 length, is the smallest component of the endocast.

155

156 *Nasal capsules and olfactory tracts*

157 The nasal capsules are large, oblong structures with a convex dorsal surface (Fig. 2). The medial  
158 edges of the nasal capsules are not parallel, instead they converge anteromedially at an angle of  
159 45 degrees (Figs. 3, 4). Unlike Thomson and Campbell (1971) we do not recognise an anterior  
160 nasal opening for a nostril present, but there is a canal exiting the capsules in their posterolateral  
161 corners; this most likely housed the profundus nerve. Challands (2015) noted that in both  
162 *Dipnorhynchus sussmilchi* and *Dipnorhynchus kurikae*, the ramus ophthalmicus profundus V  
163 enters the posterior of the nasal capsule, rather than circumventing it as seen in all other  
164 Devonian lungfishes. We see no evidence of threefold sub-divisions as reconstructed for this  
165 taxon by Thomson and Campbell (1971, Fig 29). The canals for the olfactory nerves (n.I) are  
166 expanded at their anterior extent where they join the nasal capsules, and a canal likely for either  
167 the median or lateral nasal vein, exits in a posterior direction just behind the nasal capsules (Fig.  
168 3). The olfactory tracts are broad and diverge from each other at 45 degrees, and they are  
169 proportionally shorter in *Dipnorhynchus* than in *Dipterus* or *Rhinodipterus* (Challands 2015;  
170 Clement & Ahlberg 2014). At their posterior extent there are two small rounded expansions  
171 visible in each tract that probably housed the olfactory bulbs (Fig. 5).

172

173 *Telencephalic region*

174 The telencephalic region is mostly flat dorsally, reminiscent of the condition seen in *Youngolepis*  
175 (Chang 1982), however there is a strong rise towards the pineal canal posteriorly on the dorsal  
176 margin (Fig. 2). There is a small yet distinct expansion of the telencephalic ventral edge, mostly  
177 obscured behind the large canals for the optic nerves. However, there is no evidence of a  
178 distinctive lateral telencephalic expansion like that originally reconstructed in *Dipnorhynchus*  
179 (Campbell & Barwick 1982a), nor those seen in *Chirodipterus wildungensis* (Säve-Söderbergh  
180 1952), *Rhinodipterus kimberleyensis* (Clement & Ahlberg 2014), nor extant lungfishes (Clement  
181 et al. 2015; Northcutt 2011).

182

183 *Diencephalic region*

184 The diencephalic cavity is slightly narrower than the telencephalic region and also about one-  
185 third shorter (Figs. 3, 4). Two wide, cylindrical anterolaterally-directed canals for the optic

186 nerves (n.II) exit the endocast in a ventral position at the anterior boundary of the diencephalic  
187 region. *D. sussmilchi* carries a posteroventrally long hypophyseal recess with a number of  
188 smaller, well-defined canals entering it (Figs. 2,4). The hypophyseal recesses of *Rhinodipterus*  
189 and *Dipterus* do not extend as far ventrally (Challands 2015; Clement & Ahlberg 2014), however  
190 these structures in *Youngolepis* (Chang 1982) and *Eusthenopteron* (Stensiö 1963) are of similar  
191 proportions to *Dipnorhynchus*. The hypophyseal cavity reconstructed from our scan data differs  
192 in a number of aspects from that of Campbell and Barwick (1982, fig 25). As our reconstruction  
193 is based directly on a scan of the cavity, whereas Campbell and Barwick's reconstruction was  
194 based on inferences from partly visible structures, we believe the differences reflect the  
195 limitations of the latter technique. Dorsal to the hypophysis lies a short, rounded saccus  
196 vasculosus oriented posteriorly underneath the cranial cavity (Fig. 2), similar to those seen in  
197 actinopterygians (Giles et al. 2015; Giles & Friedman 2014) or chondrichthyans (Maisey 2007).  
198 There are a number of paired canals exiting the hypophysis (Figs. 2, 4, 5); the most anterior of  
199 these extend far anterior, as far as the optic nerve canals before extending outwards laterally and  
200 likely housed the palatine arteries. The posteriorly-directed canals diverge outwards towards the  
201 trigeminal nerves and probably contained the internal carotid arteries. It is interesting to note that  
202 the canal for the internal carotid (Fig. 4) does not appear to bifurcate for a branch for the  
203 pseudobranchial artery like seen in *Dipterus* (Fig. 10b, Challands, 2015) and other  
204 stratigraphically younger lungfish. Slightly dorsal to this canal are two small canals interpreted  
205 as housing the pituitary veins. Slightly anterior to these canals are two further canals directed in  
206 an anterolateral direction that probably housed the ophthalmic arteries. Along the dorsal edge of  
207 the diencephalic region lies a broad eminence from which the pineal canal leads upwards  
208 towards the circular pineal gland in the skull roof (Fig. 2). The pineal gland is situated further  
209 anterior than that originally drawn for *Dipnorhynchus* (Campbell & Barwick 1982a). We find no  
210 obvious evidence of a parapineal gland (*contra* Campbell and Barwick 1982a), however there are  
211 a number of miniscule canals leaving from along the midline towards the skull roof dorsally in  
212 this area.

213

#### 214 *Mesencephalon*

215 The mesencephalic cavity is the shortest region of the endocast and is as narrow as the  
216 diencephalic cavity. On the lateral face of the endocast are two small paired canals exiting in

217 anterolateral directions (Fig. 2); the ventrally lower one would have housed the oculomotor nerve  
218 (n.III), and the dorsally higher one the trochlear nerve (n.IV). The ventral and dorsal edges of the  
219 mesencephalic cavity are fairly flat, about twice as high as the telencephalic region.

220

### 221 *Metencephalic and Myelencephalic cavities*

222 The metencephalic region extends from the bifurcating canals for the trigeminal nerves (n.V) to a  
223 poorly defined region posterior to the canals for the auditory nerves (n.VIII), although a distinct  
224 boundary cannot be determined. The canal for the ophthalmic nerve (n.V<sub>1</sub>) extends  
225 anterolaterally, while the combined canal for maxillary and mandibular nerves (n.V<sub>2&3</sub>) is  
226 broader and extends in a posterolateral direction. Slightly posterodorsal to this, the canal for the  
227 facial nerve (n. VII) extends laterally (Figs. 2, 5). There is a further canal anterior to and slightly  
228 ventral to the utricular recess that could have housed the abducens (n. VI) nerve (Figs. 4, 5).

229 Unlike Campbell and Barwick, we have not been able to identify the canals for the auditory (n.  
230 VIII) nerves from the data (Fig. 2). The anterior portion of the metencephalic region is of similar  
231 width to the preceding mesencephalon, though it widens laterally slightly towards its posterior  
232 extent. The ventral margin is straight but the dorsal surface is gently curved to form a convex  
233 margin forming the deepest brain region (Fig. 2). There are no prominent supraotic cavities like  
234 those seen in *Rhinodipterus* present (Clement & Ahlberg 2014). Very little can be said  
235 concerning the myelencephalic region as most of this is missing from the scan, however it  
236 appears to have a slightly lower dorsal margin than the metencephalic region but is of similar  
237 width.

238

### 239 *Labyrinth region*

240 Although the labyrinth region is incomplete, we can still observe a number of salient features.  
241 The anterior semicircular canals stand much higher than the dorsal extent of the hindbrain and  
242 *Dipnorhynchus* presumably possessed a relatively tall superior sinus (Fig. 2). There is a large  
243 ampulla on the anterior semicircular canal, and although its full extent cannot be determined, the  
244 sacculagenar pouch appears to have at least been long. The utricular recess is only moderately  
245 expanded. This is in contrast with more derived lungfishes such as *Rhinodipterus* (Clement &  
246 Ahlberg 2014), *Chirodipterus* (Säve-Söderbergh 1952), and *Dipterus* (Challands 2015), although  
247 we note it is more expanded than the reconstruction by Campbell and Barwick (1982a, fig. 25).

248

249

250 **Phylogenetic analysis**

251 The phylogenetic analysis implemented herein focuses solely on characters identifiable from  
252 cranial endocasts, and is far from comprehensive. The approach of Friedman (2007) in using the  
253 whole neurocranial complex can include a greater wealth of data than our analysis. However  
254 great care must be taken so as not to score the same character twice, once described from the  
255 neurocranium and once as an endocast feature. Indeed, the results of the phylogenetic analysis  
256 are preliminary, but it is our hope that with increasingly accessible scanning technology and a  
257 greater number of specimens examined that our character matrix will demonstrate the efficacy of  
258 endocast characters in their own right and serve as a framework for future analyses and new data,  
259 and allow workers to infer phylogeny from endocasts in cases where associated neurocranial data  
260 is not adequately provided.

261

262 The comparative endocast data used in our analysis was taken from the literature (Challands  
263 2015; Chang 1982; Clement & Ahlberg 2014; Clement et al. 2015; Holland 2014; Lu et al.  
264 2016b; Säve-Söderbergh 1952; Stensiö 1963). Although only small, the results of our analysis  
265 (Fig. 6) focusing on cranial endocast characters mostly reflect the hypotheses of relationships  
266 seen in other recent phylogenetic analyses of lungfishes and other Devonian sarcopterygians  
267 (Challands 2015; Clement 2012; Lu et al. 2016b; Qiao & Zhu 2009).

268

269 The maximum parsimony analysis produced a strict consensus tree with a score of 34 steps, and  
270 a consistency index (CI) and retention index (RI) of 0.68, homoplasy index (HI) of 0.32, and a  
271 rescaled consistency index (RCI) of 0.46. *Qingmenodus* is the most basal taxon above the  
272 outgroup *Diplocercides*. The tetrapodomorphs *Gogonasus* and *Eusthenopteron* form a clade as  
273 sister group to the lungfish total group (Dipnomorpha). *Youngolepis* is the most basal taxon in  
274 the Dipnomorpha, with *Dipnorhynchus* the most basal of the Dipnoi. *Dipterus*, *Chirodipterus*  
275 and *Rhinodipterus* are more derived occupying successive branches, with *Neoceratodus*  
276 comprising a crownward position (Fig. 6).

277

278 The results of the phylogenetic analysis do support the use of endocast characters in analyses,  
279 either in isolation or in conjunction with other morphological characters. Although virtual  
280 palaeoneurology is still its infancy, especially with respect to fishes, cranial endocasts show great  
281 potential with which to support hypotheses of phylogeny.

282

## 283 **DISCUSSION**

### 284 **a) The *Dipnorhynchus susmilchi* endocast**

285 The first reconstruction of the cranial endocast of *Dipnorhynchus* was drawn directly from  
286 broken specimens and inferring internal morphology without the aid of scanning technology  
287 (Campbell & Barwick 1982a), similar to the method used for *Chirodipterus wildungensis* (Säve-  
288 Söderbergh 1952). In comparison with that reconstruction, we largely agree with most characters  
289 including the placement of the cranial canals and general proportions of brain regions. However  
290 the most striking point of difference is that there is no large recess for a separate para-pineal  
291 canal visible in our scan data (*contra* Campbell & Barwick 1982, fig 25). There is a large,  
292 obvious space for the pineal canal (Fig. 1b), but our specimen of *Dipnorhynchus susmilchi*  
293 appears to lack any separate para-pineal canal. Furthermore, the position of the pineal gland is  
294 placed further anteriorly in our reconstruction compared to that of Campbell and Barwick (1982),  
295 at the level of the optic nerve canals rather than at the level of n. IV; this is more in line with the  
296 generalized gnathostome condition. There are, however, a number of minute canals exiting the  
297 cranial cavity dorsally in this dorsal region of the forebrain that may have been related to the  
298 pineal organ.

299

300 Another significant difference is the lack of any noticeable lateral expansion in the telencephalic  
301 region in contrast to that shown by Campbell and Barwick (1982). Instead the narrow forebrain  
302 appears similar to that of the Early Devonian dipnomorph, *Youngolepis* (Chang 1982, fig. 19) in  
303 this respect though the presence of a small ventral expansion in *Dipnorhynchus* is more  
304 reminiscent of the condition seen in *Dipterus* (Challands 2015). Similarly, Campbell and  
305 Barwick (1982) did not reconstruct an utricular recess outwardly differentiated from the  
306 sacculolagenar pouch. However, we find differentiated sacculolagenar – utricular recesses. The  
307 condition is more similar to that reconstructed for *Dipnorhynchus kurikae* by the same authors  
308 (Campbell & Barwick 2000, fig. 4).

309

310 New characters that can be identified in our scan data include the size and shape of the nasal  
311 capsules, the position of the nasal vein (Fig. 1), as well as details concerning the canals exiting  
312 the hypophysis. We are able to distinguish and trace the course of the canals for the palatine,  
313 ophthalmic and internal carotid arteries, as well as the canal for the pituitary vein (Figs. 3, 4).

314

315

### 316 **b) Comparison with other sarcopterygians**

317 In Figure 6 the updated endocast of *Dipnorhynchus* is compared with that of other Devonian  
318 lungfishes from which a complete cranial endocast is known, as well as the Early Devonian  
319 dipnomorph, *Youngolepis*, two tetrapodomorph taxa (*Gogonasus* and *Eusthenopteron*), the  
320 onychodont *Qingmenodus*, and *Diplocercides* the coelacanth. In the forebrain, the slight ventral  
321 expansion of the telencephalic region in *Dipnorhynchus susmilchi* contrasts with the more  
322 pronounced expansion in the stratigraphically younger *Chirodipterus wildungensis* and  
323 *Rhinodipterus kimberleyensis*. This trend and its implications have already been discussed  
324 (Clement & Ahlberg 2014). It was proposed that this trend of increasing size of the telencephalic  
325 region might correlate with an increased reliance on olfaction in lungfishes over time. However,  
326 it may also reflect an increased capacity to navigate environmentally complex ecosystems or  
327 social systems, as seen in chondrichthyans (Yopak et al. 2007). Two slight bulges at the base of  
328 the olfactory nerves (see Fig. 5) suggest that the olfactory bulbs were sessile rather than  
329 pedunculate. Relatedly, we believe that the identification of the olfactory bulbs in *Rhinodipterus*  
330 may have been originally overlooked; a slight bulge in telencephalic region just posterior of the  
331 olfactory canals could represent these (Clement and Ahlberg 2014, fig. 2) as is the condition  
332 interpreted in *Dipterus* also (Challands 2015).

333

334 Posterior to the pineal recess in *Dipnorhynchus* and *Dipterus* (but apparently lacking in  
335 *Chirodipterus*) lies a small bulge on the dorsal surface of the hindbrain region of the endocast.  
336 Challands (2015, fig. 9) tentatively identified this as the space for the optic lobes in *Dipterus*.  
337 Campbell and Barwick (1982) reconstructed a single dorsally oriented canal in this region, but  
338 we again could not locate such a canal in the tomographic data. Unfortunately this region of the  
339 skull was damaged in *Rhinodipterus* so its morphology cannot be determined for this taxon.

340

341 As previously discussed (Challands 2015; Clement & Ahlberg 2014), Devonian and later  
342 lungfishes show a trend of increasing size of the utricular recess relative to the sacculolagena,  
343 and that of *Dipnorhynchus* remains small and relatively undifferentiated in comparison to later  
344 taxa. Not surprisingly, it closely resembles that of *Dipnorhynchus kurikae* (Campbell and  
345 Barwick 2000, fig. 5). Moreover, *Dipterus* and *Rhinodipterus* both possess a small notch  
346 demarcating the lagenar and saccular portions of the labyrinth region, while this is absent in  
347 *Chirodipterus* and extant lungfishes (Clement and Ahlberg 2014, fig. 4). All of the lungfish, as  
348 well as *Youngolepis*, *Gogonasmus* and *Eusthenopteron* possess a high superior sinus that extends  
349 dorsally above the endocranial roof.

350

351 Overall the updated endocast of *Dipnorhynchus* closely resembles that of *Youngolepis* and  
352 *Diplocercides* in possessing a ventrally-extensive hypophyseal recess, and in lacking any  
353 telencephalic lateral expansion. However the emergence of a differentiated utricular recess,  
354 ventral expansion of the telencephalon (albeit only slight) and a combined anterodorsally-  
355 oriented para-pineal gland resembles those of stratigraphically younger lungfish. These latter  
356 features lend support to the primitive placement of *Dipnorhynchus* within the Dipnoi more  
357 basally than other lungfish for which the endocranial anatomy is known.

358

### 359 **c) Evolutionary significance**

360 The cranial endocast of *Dipnorhynchus* exhibits conditions typical for primitive sarcopterygians.  
361 A small utricular recess is shared with *Youngolepis*, *Eusthenopteron*, *Diplocercides* and  
362 *Qingmenodus* implying that the expansion of the utricular recess is a derived condition  
363 (synapomorphy) within the dipnoans. Also, unlike more derived lungfishes (*Chirodipterus*,  
364 *Rhinodipterus*, *Neoceratodus*), *Dipnorhynchus* retains a buccohypophyseal opening and lacks  
365 separate foramina for the internal carotid artery and efferent pseudobranchial arteries. On the  
366 other hand, *Dipnorhynchus* demonstrates the derived condition in lacking an intracranial joint,  
367 and shows a sinus superior that obviously extends above the roof of the rhombencephalon; a  
368 character first observed in early actinopterygians (Giles et al. 2016), and the tetrapodomorphs  
369 *Eusthenopteron* and *Gogonasmus*, but absent in *Qingmenodus* and *Diplocercides* (Fig. 6).

370

371 Of further note is the proportion of the hindbrain, the rhombencephalon, relative to other  
372 Devonian sarcopterygians. *Dipnorhynchus* and all subsequent dipnoans demonstrate a shortening  
373 of the distance between the hypophyseal recess and rhombencephalon, a state more akin to basal  
374 actinopterygians such as *Mimipiscis* (Giles & Friedman 2014). As such, this character appears to  
375 be a synapomorphy for the Dipnoi, convergent with the condition in Actinopterygii (Giles et al.  
376 2016), the shortening likely related to the loss of the intracranial joint (also seen in the  
377 dipnomorph *Youngolepis*). Lu et al. (2016b) noted that the rhombencephalon in Devonian  
378 sarcopterygians is generally well-developed to the anterior, with the facial nerve (n.VII) being  
379 located well behind the trigeminal complex and anterior to the labyrinth. They tentatively  
380 attributed this expansion to an increased demand for functional sensitivity processed in this  
381 region of the brain (e.g. motor control in the pons and cerebellum), which if correct, has reverted  
382 to the primitive actinopterygian condition in the first appearance of the Dipnoi. Other  
383 morphological correlates with well-developed facial functional sensitivity are, however, still  
384 present in the Dipnoi such as in *Dipterus* where Challands (2015) noted the extensive innervation  
385 in the rostral region by the facial nerve (n.VII) as well as the lateral line by the same nerve  
386 complex. Such patterns illustrate the complexities involved in simply attributing endocast  
387 volume to increased functional processing for a certain region of the brain. Inferring functional  
388 evolutionary trajectories from endocast volumes, especially where demarcation between regions  
389 is to a certain extent subjective, is, at best, speculative unless the nervous and functional systems  
390 are considered as a whole.

391

392

### 393 **CONCLUDING REMARKS**

394 Here we present the oldest lungfish cranial endocast known, that of *Dipnorhynchus sussmilchi*,  
395 from the Early Devonian of Australia, as reconstructed from tomographic data. The virtual  
396 endocast presented herein largely confirms the previous depiction by Campbell and Barwick  
397 (1982a) however there exist a number of notable differences. These include the lack of a separate  
398 para-pineal gland, and similarly the lack of any lateral expansion of the telencephalon. However  
399 the presence of a small, but differentiated utricular recess, and new details of the canals exiting  
400 the ventrally-extensive hypophysis are revealed.

401

402 As only the fourth Devonian lungfish endocast known, *Dipnorhynchus* represents a significant  
403 contribution to the field of vertebrate palaeoneurology. However, to be able to draw more useful  
404 conclusions concerning dipnoan phylogeny or function we must continue to expand our  
405 knowledge base. Neurocrania (and consequently their associated cranial endocasts) are  
406 morphologically complex and phylogenetically informative structures, as has already been well  
407 illustrated for lungfishes (Friedman 2007). We present the first character matrix based solely on  
408 endocast characters for lungfishes. The analysis supports a basal placement of *Dipnorhynchus*  
409 within the dipnoan stem group in agreement with other recent phylogenetic analyses  
410 demonstrating the robustness of endocasts alone in creating instructive phylogenetic hypotheses.

411

412

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420

421

#### 422 **FIGURE CAPTIONS**

423 **Figure 1. Map showing localities yielding Early Devonian dipnorhynchid taxa in south-**  
424 **eastern Australia.**

425

426 **Figure 2. *Dipnorhynchus sussmilchi* cranial endocast in lateral view.** A, virtual  
427 reconstruction; and B, schematic illustration of ANU 18815; C, reproduction of *D. sussmilchi*  
428 endocast from Campbell and Barwick (1982, fig. 25a).

429

430 **Figure 3. *Dipnorhynchus sussmilchi* cranial endocast in dorsal view.** A, virtual  
431 reconstruction; and B, schematic illustration.

432

433 **Figure 4. *Dipnorhynchus sussmilchi* cranial endocast in ventral view.** A, virtual  
434 reconstruction; and B, schematic illustration.

435

436 **Figure 5. *Dipnorhynchus sussmilchi* cranial endocast in anterolateral view.** A, virtual  
437 reconstruction; and B, schematic illustration.

438

439 **Figure 6. Phylogenetic relationships of selected sarcopterygians as interpreted from cranial**  
440 **endocast morphology.** A, the Late Devonian coelacanth *Diplocercides kayseri* (from Stensiö  
441 1963, fig. 45); B, the Early Devonian onychodont *Qingmenodus yui* (from Lu et al. 2016, fig. 2);  
442 the Late Devonian tetrapodomorphs C, *Gogonasus andrewsae* (from Holland 2014, figs. 22,23);  
443 and D, *Eusthenopteron foordi* (Stensiö 1963, fig. 50); E, the Early Devonian dipnomorph  
444 *Youngolepis praecursor* (from Chang 1982, fig. 19); F, the Early Devonian dipnoan  
445 *Dipnorhynchus sussmilchi* (ANU 18815); G, the Middle Devonian dipnoan *Dipterus*  
446 *valenciennesi* (from Challands 2015, fig. 9); the Late Devonian dipnoans H, *Chirodipterus*  
447 *wildungensis* (from Säve-Söderbergh 1952, fig. 9); and I, *Rhinodipterus kimberleyensis* (WAM  
448 09.6.149); J, the extant Australian lungfish *Neoceratodus forsteri* (from Clement et al. 2015, fig.  
449 6).

450

#### 451 SUPPLEMENTARY INFORMATION FIGURE CAPTIONS

452 **Figure 1. Two slices through the CT scan data of *Dipnorhynchus sussmilchi* showing**  
453 **quality of scans, and with certain features labelled.**

454

455

456

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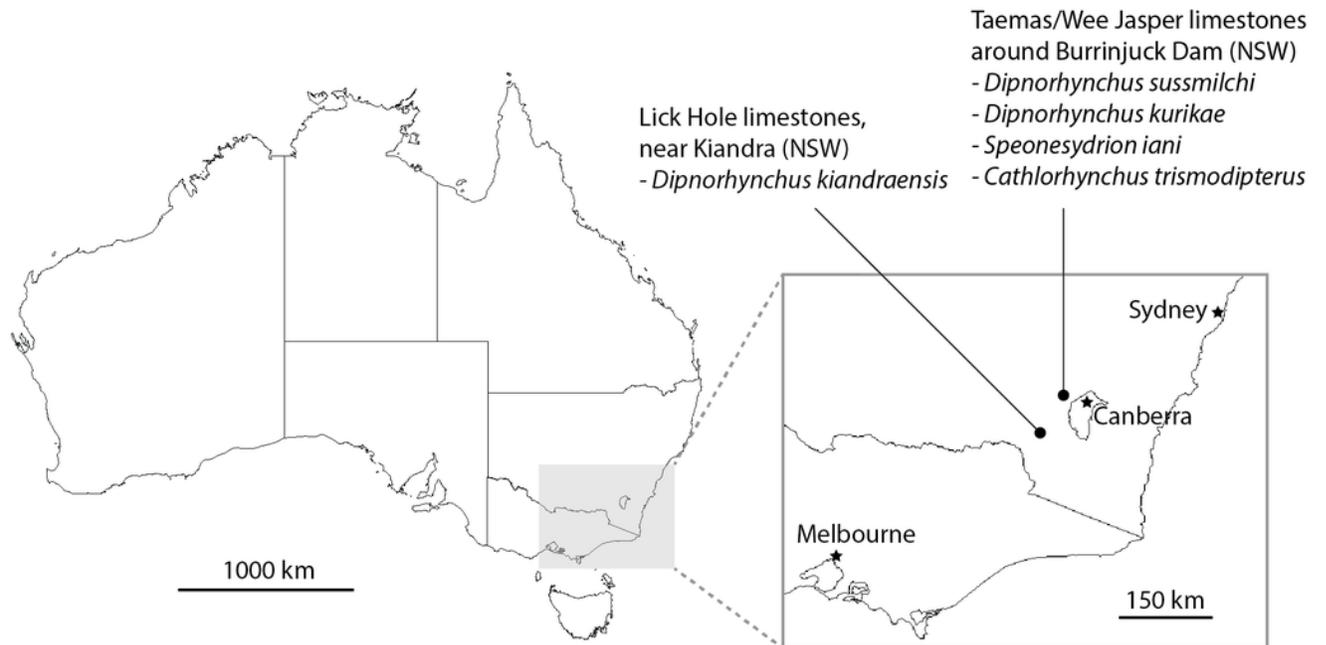
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# Figure 1

Map showing localities yielding Early Devonian dipnorhynchid taxa in south-eastern Australia.

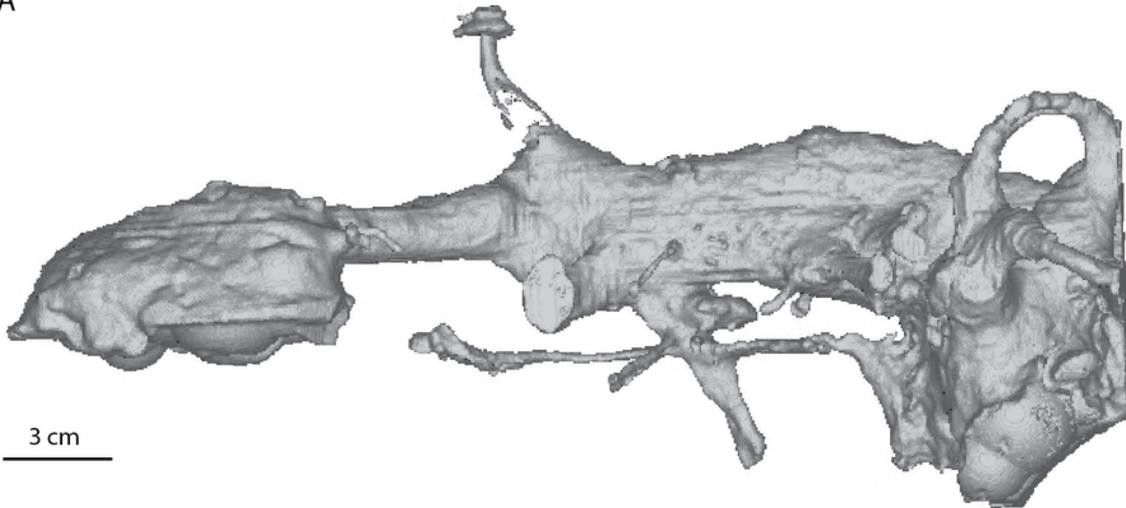


## Figure 2

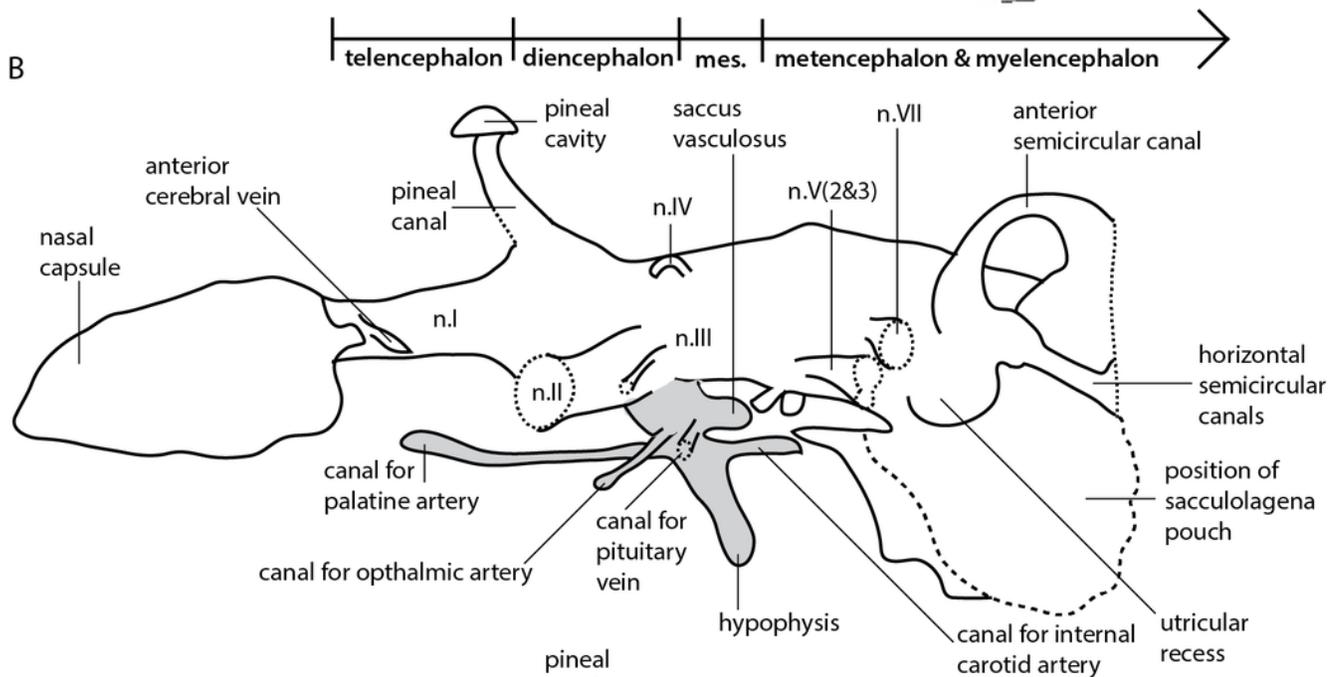
*Dipnorhynchus sussmilchi* cranial endocast in lateral view.

A, virtual reconstruction; and B, schematic illustration of ANU 18815; C, reproduction of *D. sussmilchi* endocast from Campbell and Barwick (1982, fig. 25a).

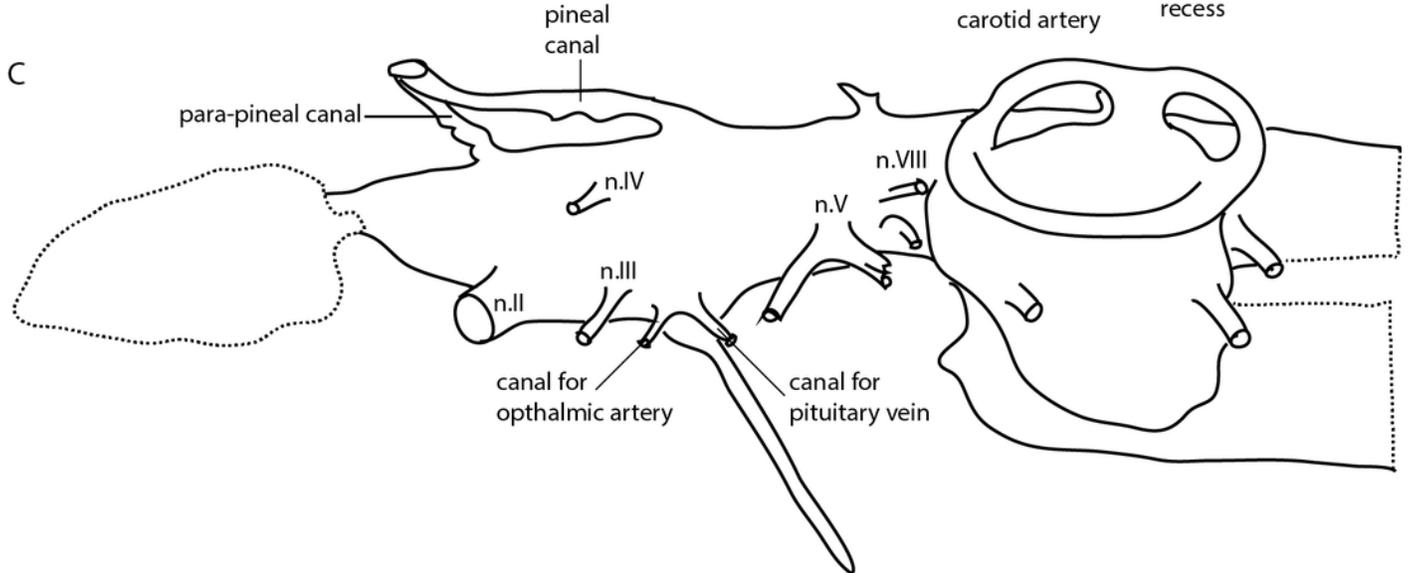
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B



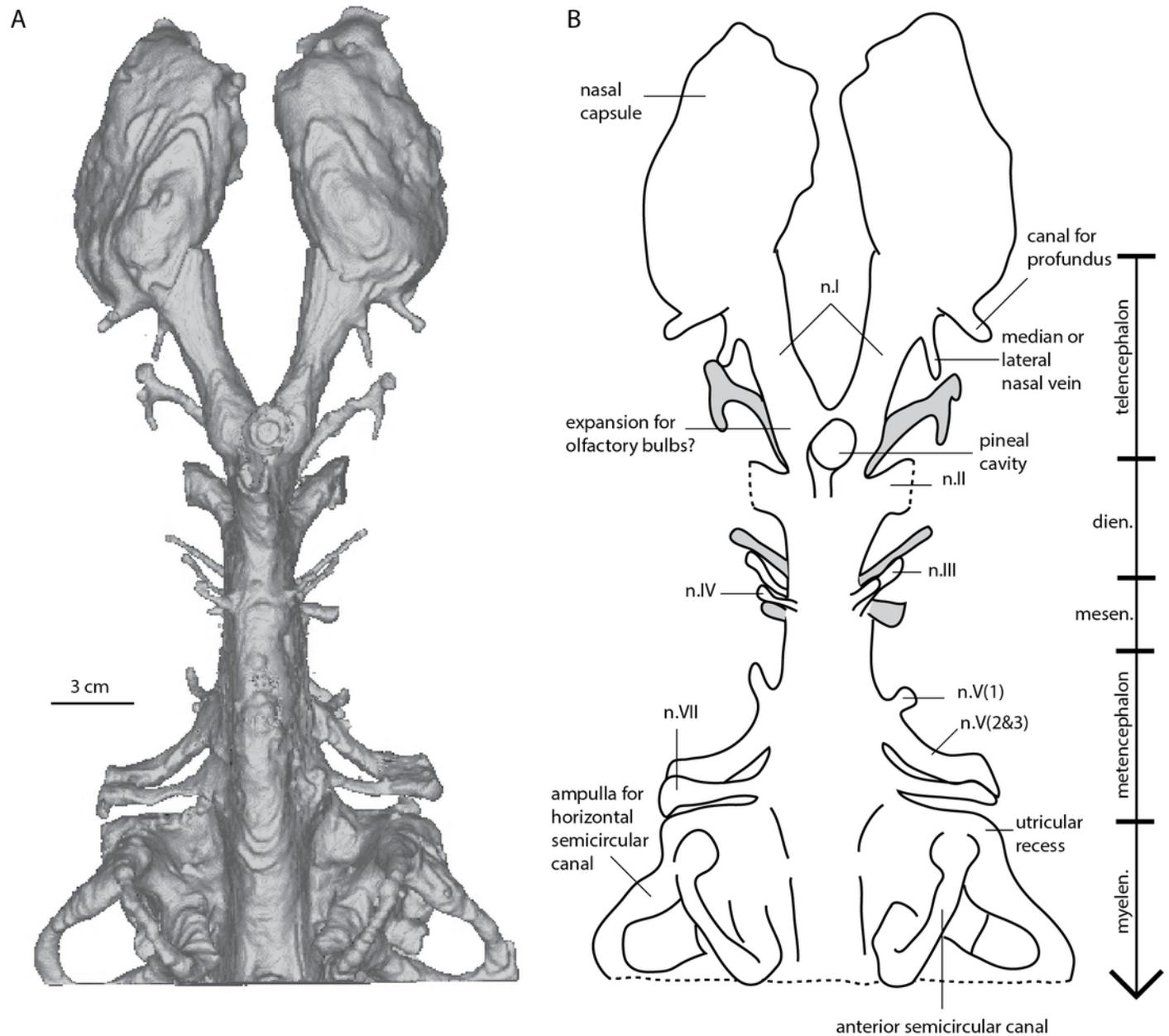
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# Figure 3

*Dipnorhynchus susmilchi* cranial endocast in dorsal view.

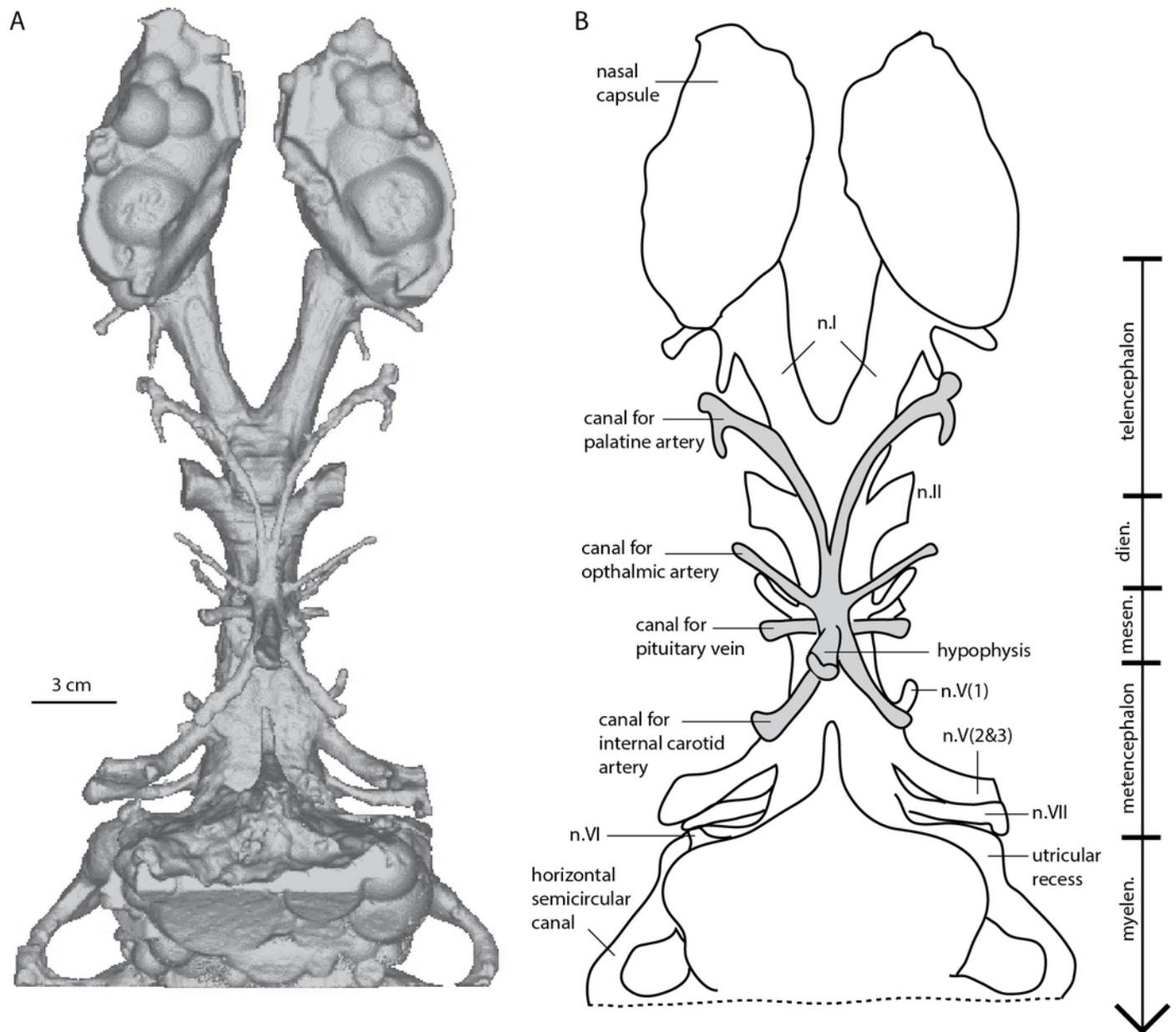
A, virtual reconstruction; and B, schematic illustration.



## Figure 4

*Dipnorhynchus sussmilchi* cranial endocast in ventral view.

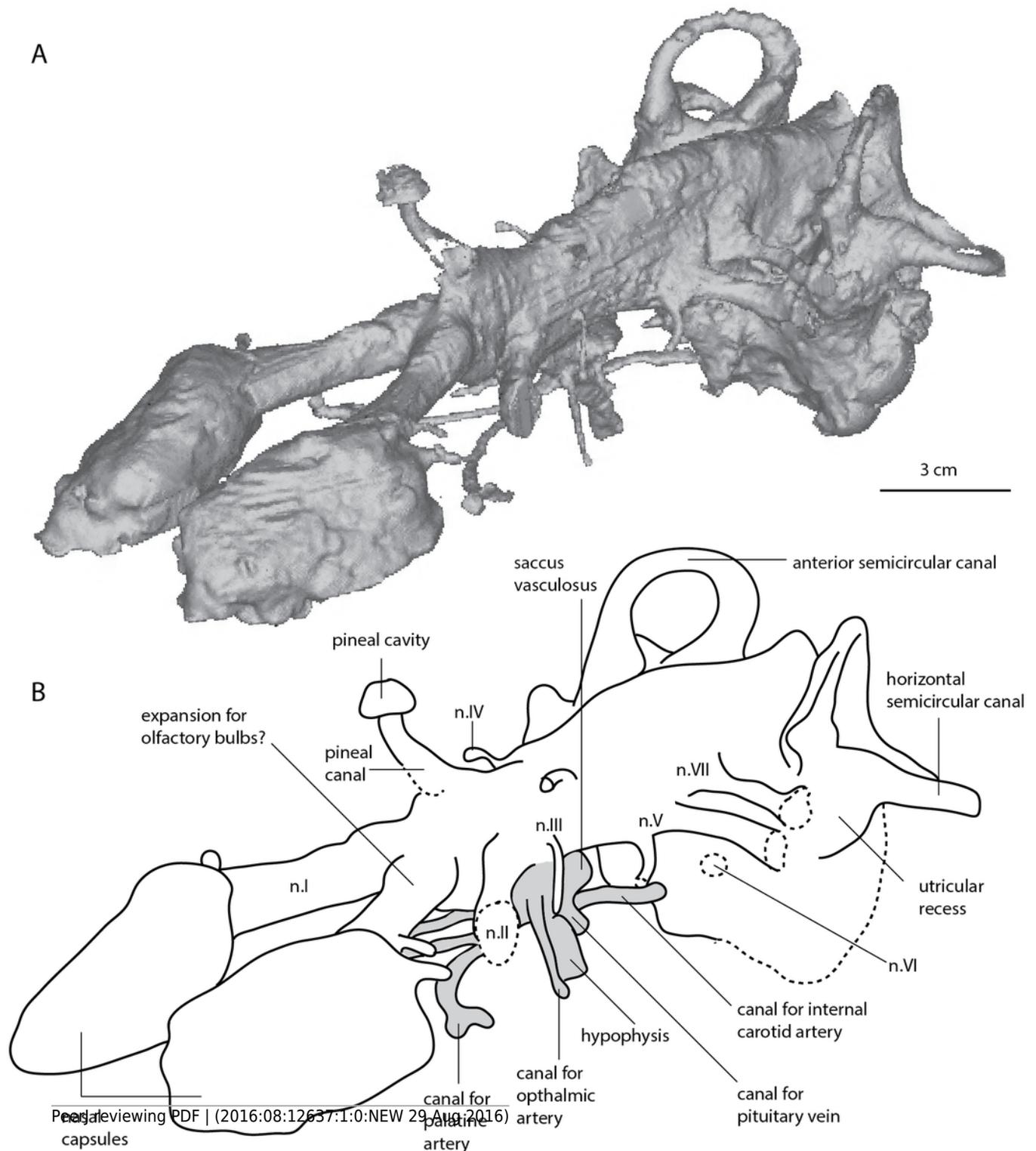
A, virtual reconstruction; and B, schematic illustration.



# Figure 5

*Dipnorhynchus susmilchi* cranial endocast in anterolateral view.

A, virtual reconstruction; and B, schematic illustration.



## Figure 6

Phylogenetic relationships of selected sarcopterygians as interpreted from cranial endocast morphology.

A, the Late Devonian coelacanth *Diplocercides kayseri* (from Stensiö 1963, fig. 45); B, the Early Devonian onychodont *Qingmenodus yui* (from Lu et al. 2016, fig. 2); the Late Devonian tetrapodomorphs C, *Gogonasus andrewsae* (from Holland 2014, figs. 22,23); and D, *Eusthenopteron foordi* (Stensiö 1963, fig. 50); E, the Early Devonian dipnomorph *Youngolepis praecursor* (from Chang 1982, fig. 19); F, the Early Devonian dipnoan *Dipnorhynchus sussmilchi* (ANU 18815); G, the Middle Devonian dipnoan *Dipterus valenciennesi* (from Challands 2015, fig. 9); the Late Devonian dipnoans H, *Chirodipterus wildungensis* (from Säve-Söderbergh 1952, fig. 9); and I, *Rhinodipterus kimberleyensis* (WAM 09.6.149); J, the extant Australian lungfish *Neoceratodus forsteri* (from Clement et al. 2015, fig. 6).

